

# Microphytobenthic Potential Productivity Estimated in Three Tidal Embayments of the San Francisco Bay: A Comparative Study

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**ABSTRACT:** In this paper we describe a three-step procedure to infer the spatial heterogeneity in microphytobenthos primary productivity at the scale of tidal estuaries and embayments. The first step involves local measurement of the carbon assimilation rate of benthic microalgae to determine the parameters of the photosynthesis-irradiance (P-E) curves (using non-linear optimization methods). In the next step, a resampling technique is used to rebuild pseudo-sampling distributions of the local productivity estimates; these provide error estimates for determining the significance level of differences between sites. The third step combines the previous results with deterministic models of tidal elevation and solar irradiance to compute mean and variance of the daily areal primary productivity over an entire intertidal mudflat area within each embayment. This scheme was applied on three different intertidal mudflat regions of the San Francisco Bay estuary during autumn 1998. Microphytobenthos productivity exhibits strong (ca. 3-fold) significant differences among the major sub-basins of San Francisco Bay. This spatial heterogeneity is attributed to two main causes: significant differences in the photosynthetic competence (P-E parameters) of the microphytobenthos in the different sub-basins, and spatial differences in the phase shifts between the tidal and solar cycles controlling the exposure of intertidal areas to sunlight. The procedure is general and can be used in other estuaries to assess the magnitude and patterns of spatial variability of microphytobenthos productivity at the level of the ecosystem.

## Introduction

Two communities of microalgae contribute to primary production in tidal estuaries: phytoplankton and microphytobenthos. From decades of study we have developed a general understanding of the fundamental features of estuarine phytoplankton ecology including the mechanisms, magnitude, and patterns of variability of primary production (review in Cloern 1996). We know that phytoplankton primary production can vary (by up to an order of magnitude) along the river-ocean continuum of some estuaries (Cloern 1987). Our history of studying the microphytobenthos is much shorter (review in Guarini et al. 2000), and only a few studies have attempted to develop a global understanding of the population ecology and, particularly, the production dynamics of this benthic microalgal community (Admiraal 1984; Pinckney and Zingmark 1993; Guarini et al. 1999; Underwood and Krompkamp 1999).

The intertidal microphytobenthos includes an assemblage of motile benthic diatoms (mainly pennate) that migrate vertically upward to the sedi-

ment surface at the beginning of the daytime emersion period and downward at the end (Serôdio et al. 1998). Because of high turbidity in shallow areas which limits light penetration (Alpine and Cloern 1988), microphytobenthic primary production mostly occurs on the surface of intertidal mudflats during the daytime emersion periods. Light attenuation into the mud is so strong (Kühl et al. 1994) that benthic microalgae primary production is mainly performed in a biofilm at the surface of the sediment (Guarini et al. 1999, 2000). At the beginning of each daytime emersion period, the biomass at the surface of the mud quickly reaches a saturation value (Guarini et al. 1999, 2000) so that microphytobenthos production dynamics is mostly governed by the biomass-specific productivity of benthic microalgae and dynamic changes in light exposure.

We describe a model-based approach for assessing the macro-scale potential variability of microphytobenthos productivity in tidal estuaries and illustrate the approach with data collected across the habitat gradients of San Francisco Bay. Community primary productivity is described by the assimilation rate  $P^B$ , i.e., the daily carbon fixation rate per unit of chlorophyll biomass [ $\text{mg C} (\text{mg chl d})^{-1}$ ].

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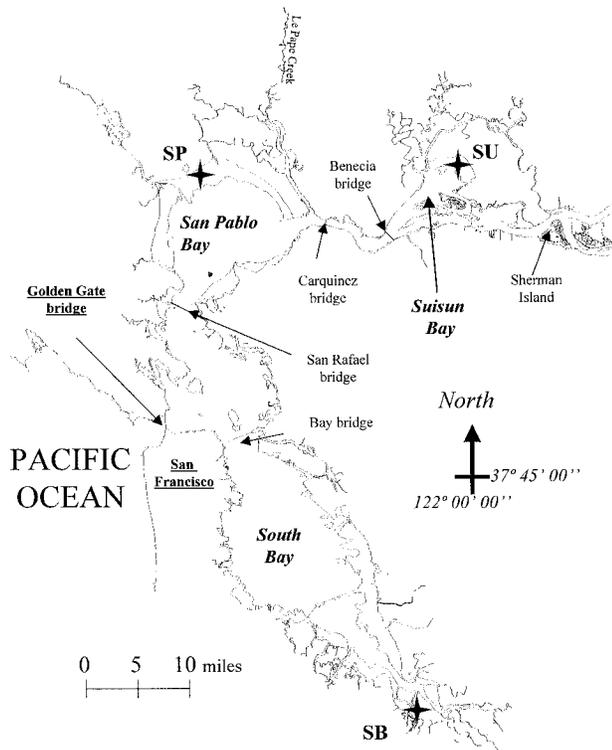


Fig. 1. Location of the 3 primary embayments of the San Francisco Bay estuary. Boundaries are represented by the bridges and by Sherman Island in the eastern part of Suisun Bay. Stars represent sampling stations on intertidal mudflats within each embayment and are labeled SB, SP, and SU for South Bay, San Pablo Bay, and Suisun Bay, respectively.

Spatial variability of  $P^B$  reflects not only the variability of potential productivity of the microalgal community, quantified by parameters of a photosynthesis-irradiance (P-E) function, but also the spatial variability induced by the interactions between the solar cycle and the tidal propagation as they regulate the availability of sunlight energy to the intertidal microphytobenthos (Underwood and Krompkamp 1999). Both modes of variability are encompassed in the present note, by identifying parameters of a P-E function, and modeling the daily cycle of light exposure to the intertidal surface. Our purpose is to combine deterministic light availability modeling with a Monte-Carlo method (Rubinstein 1981) assessing the variability of microphytobenthos productivity estimates and then to compare the relative daily primary productivity in three different intertidal habitats of San Francisco Bay.

## Methods and Study Design

### STUDY SITE

San Francisco Bay includes large areas of intertidal habitat in three sub-basins that could present

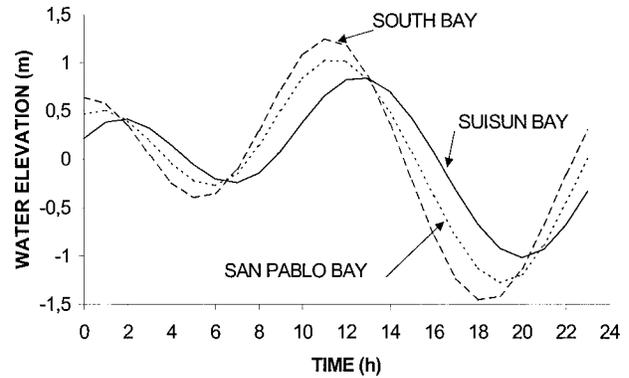


Fig. 2. Example of phase and amplitude differences of the tidal propagation between South Bay, San Pablo Bay, and Suisun Bay. Results are provided for the year 1998 by a tidal-harmonic model using constants calculated for each embayment (see text). The hourly values of the water elevation combined with the bathymetry of intertidal mudflats give emersion and submersion durations at each node of a  $0.1 \times 0.1$  km spatial mesh grid.

differences in microphytobenthos photosynthesis. The San Francisco Bay system (Fig. 1) includes two connected, but distinct, estuaries: the North Bay is a partially-stratified estuary strongly influenced by inputs from the Sacramento and San Joaquin Rivers and the South Bay is an urbanized lagoon-type estuary. The North Bay includes two embayments with fringing intertidal zones: San Pablo Bay, which is relatively influenced by sea water; and Suisun Bay, which is oligohaline and influenced by its proximity to the riverine inputs of freshwater and sediments. Intertidal areas of the three embayments are  $6 \text{ km}^2$  for Suisun Bay,  $45 \text{ km}^2$  for San Pablo Bay, and  $86 \text{ km}^2$  for South Bay.

Phytoplankton dynamics differ greatly among the subsystems of San Francisco Bay. Annual phytoplankton primary production is only about  $20 \text{ g C m}^{-2}$  in Suisun Bay (Alpine and Cloern 1992) but over  $200 \text{ g C m}^{-2}$  in the lower South Bay (Cloern 1987). This macro-scale variability of phytoplankton production is partly a result of spatial variations in turbidity. The light available for the microphytobenthos could further be regulated through a very different mechanism—the modulation of the tidal wave as it propagates into the estuary (Fig. 2). The North Bay tidal wave is progressive, so the tidal amplitude becomes damped and the phase delayed as the tide propagates into the northern estuary (Walters et al. 1985). Basin morphometry of South Bay sets up a standing wave in which tidal amplitude grows and the phase lags are small. We hypothesize that these spatial differences in tidal dynamics act as a source of regional (i.e., between sub-basins) variation, by inducing differences in

light exposure regimes over the intertidal mudflats in the three embayments of San Francisco Bay.

#### SAMPLING AND LABORATORY ANALYSES

We considered two scales of variability: a small or local scale ( $\sim 10\text{--}1,000$  m): at this scale, changes in microalgal community composition and physiological state are assumed to be random, and re-suspension, transport, and sedimentation of surficial sediments act as dispersion processes; and a regional or sub-basin scale ( $\sim 10\text{--}100$  km): the spatial variability is induced by the larger scale gradients of habitat, community composition, or physiological state of the microphytobenthos. To investigate the small-scale variability, we collected two different samples from the same location (within  $\sim 200$  m) of individual mudflats. To measure sub-basin variability, we sampled one location on mudflats in the lower South Bay (September 8, 1998), Suisun Bay (October 6, 1998), and San Pablo Bay (September 22, 1998); meteorological conditions were stable over the sampling period.

Samples were collected by scraping the mud surface randomly in a  $\sim 2\text{-m}^2$  area at low tide. Samples were kept in the dark during transit to the laboratory, where mud was mixed gently, spread in flat trays to a depth of  $\sim 1$  cm, and covered with a  $64\text{-}\mu\text{m}$  mesh nylon screen. A silica gel was prepared with filtered sea water and combusted silica powder (between 60 and  $200\ \mu\text{m}$ ), and the gel was spread on the nylon screen to collect benthic diatoms as they migrated vertically from the sediment. Migration was induced by holding the tray under light for several hours. The silica gel was then gently scraped and sieved with a  $64\text{-}\mu\text{m}$  screen to separate microalgae from the silica powder. The harvested cells were suspended in filtered seawater and homogenized with a magnetic stirrer. Separate aliquots of the cell suspension were used to measure photosynthesis and chlorophyll *a* (chl *a*) concentration (by fluorometry; Parsons et al. 1984), and for preservation (Lugol's solution) and later microscopic examination for taxonomic identification. This specific composition is described by the cell density (number of cells  $\text{ml}^{-1}$ ) and the calculated biovolume ( $\mu\text{m}^3\ \text{ml}^{-1}$ ), assuming that the microalgae can be assimilated as double cones and using the formula  $V(\mu\text{m}^3) = (\pi/6) d^2 L$  to calculate their mean-individual volume from the half mean length *L* ( $\mu\text{m}$ ) and the maximum mean diameter *d* ( $\mu\text{m}$ ).

The photosynthetic activity of the microphytobenthos, a measure of the potential productivity, was measured as the rate of  $^{14}\text{C}$ -bicarbonate uptake (Darley et al. 1976), using a photosynthetron (Lewis and Smith 1983) to provide a gradient of light levels between 0 and  $1,600\ \mu\text{E m}^{-2}\ \text{s}^{-1}$ . Quantum

fluxes ( $\mu\text{E m}^{-2}\ \text{s}^{-1}$ ) were converted to energy ( $\text{W m}^{-2}$ ) according to the equivalence  $1\ \mu\text{E m}^{-2}\ \text{s}^{-1} = 4.15\ \text{W m}^{-2}$  (Cullen 1990); energy is then described as photosynthetic active radiation (PAR). Three-ml aliquots of the cell suspension were incubated in 20-ml scintillation vials for 30 min at  $25^\circ\text{C}$  (near the optimal temperature for photosynthesis; Blanchard et al. 1997). After incubation, photosynthesis was stopped and residual  $^{14}\text{C}$  bicarbonate was removed by the addition of 0.2 N HCl. Radiocarbon activity was measured with a Wallac 1209 RackBeta liquid scintillation counter. Total  $\text{CO}_2$  was measured in water samples acidified with 6 N HCl; evolved  $\text{CO}_2$  was measured with a Perkin Elmer Sigma 2000 gas chromatograph. All photosynthetic rates were normalized to chl *a* concentration to give the biomass-specific rate of carbon assimilation,  $p^B$ .

#### PARAMETERS OF THE PHOTOSYNTHESIS-IRRADIANCE FUNCTION

The following function (Jassby and Platt 1976) was fitted to the experimental data:

$$p^B = p_{\max}^B \tanh\left(\frac{E}{E_k}\right) \quad (1)$$

where  $p^B$  is the hourly carbon assimilation rate ( $\text{mg C (mg chl } a)^{-1}\ \text{h}^{-1}$ ),  $p_{\max}^B$  is the maximum carbon assimilation rate ( $\text{mg C (mg chl } a)^{-1}\ \text{h}^{-1}$ ),  $E_k$  is the light saturation parameter in  $\text{W m}^{-2}$  ( $= p_{\max}^B/\alpha$ , where  $\alpha$  is the photosynthetic efficiency), and  $E$  is the PAR ( $\text{W m}^{-2}$ ), in the spectral range between 350 and 700 nm. The vector of parameter estimates  $\theta = \{\hat{p}_{\max}^B, \hat{E}_k\}$  was obtained by minimization of an ordinary least-squares criterion performed by a simple algorithm (Nelder and Mead 1965).

Since the goal of the study is to compare the microphytobenthos productivity of major sub-basins in San Francisco Bay, it is first necessary to quantify the local (within sub-basin) variability of P-E curve parameter estimates; a classical approach (e.g., the ANOVA-based approach) would have required several local replicates of P-E curve fitting. In the present study however, only two P-E experiments per sub-basin are available, and a bootstrap (Fig. 3; Efron and Tibshirani 1993) was applied in order to compute the variance-covariance matrix  $\text{V}\hat{\text{a}}\text{r}(\theta)$ .

A given local data set is summarized by the fitted model  $\{p_i^B = \varphi(E_i, \theta) + e_i, i = 1, n\}$  where  $\varphi(E_i, \theta)$  is given by Eq. 1, *n* is the number of observed pairs ( $p_i^B, E_i$ ),  $\theta$  is the vector of parameter estimates, and  $e_i$  is the residual. Owing to the good confidence we have in the adequacy of the model to describe the P versus E relationship, we resampled the centered residuals  $\eta_i = e_i - \bar{e}$ , assuming they are in-

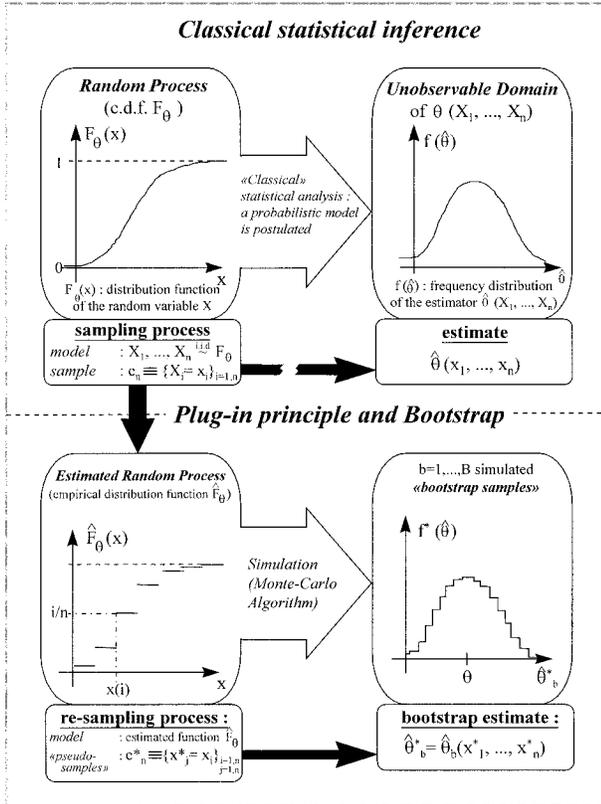


Fig. 3. The principle of the bootstrap method is to estimate the parameter distribution function from only one set of observations. The upper part of this figure presents the classical scheme of statistical inference, which allows estimates of parameters of a probabilistic model (e.g., mean and variance for a normal distribution function) from a series of samples. The probabilistic model describes an unknown random process. In the bootstrap procedure, the empirical distribution function  $\hat{F}_\theta$  is simulated from the available data set (the set of observations  $c_n$ ), which contains all the information about  $F_\theta$ , according to the theorem of sufficiency. This empirical distribution function is used to define the plug-in estimate of  $\theta = t(F_\theta)$ , called  $\theta^* = t(\hat{F}_\theta)$ .

dependent of the predictor  $E$ . Bootstrap samples were obtained with a Monte-Carlo algorithm (Fig. 3), which generated  $M$  ( $= 500$ ) independent realizations of the random multinomial vector  $P^* \sim \text{Mult}(n, p^0)/n$ . For each bootstrap sample, we then computed a bootstrap replicate  $\theta_m^* = \theta(P_m^*)$ ,  $m = 1, \dots, M$ , allowing us to estimate both the mean and the variance-covariance of the P-E parameters.

#### ESTIMATION OF MICROPHYTOBENTHOS POTENTIAL PRODUCTIVITY AT THE ECOSYSTEM LEVEL

The second step of our analysis was to use the P-E functions to estimate daily photosynthetic productivity across the intertidal habitats of South Bay, San Pablo Bay, and Suisun Bay. We presume that the P-E parameter estimates are valid for the fall

season only, and we used these to estimate the mean daily carbon assimilation for the period September 21 to December 21. This calculation requires information about the bathymetry of each mudflat, the daily changes in tidal elevation, and the diurnal cycle of solar irradiance. We defined the intertidal area as the zone emerged or submerged at least once per year. The bathymetry of each mudflat was represented with a regular  $0.1 \times 0.1$  km grid, derived from interpolations (inverse weighted distance) of the depth soundings available for San Francisco Bay (NOAA 1998). Tidal elevations were computed every hour, using a tidal-harmonic model calibrated with year-long stage records in South, San Pablo, and Suisun Bays (Cheng and Gartner 1984). Incident light energy was calculated every hour with the model of Frouin et al. (1989), calculating clear-sky light energy ( $R_S$  in  $W m^{-2}$ ) as:

$$R_S = R_0 \sin(h) (1 - A) \quad (2)$$

where  $R_0$  is the solar constant in the spectral range 350–700 nm ( $R_0 = 584.9 W m^{-2}$ ),  $A$  is the albedo (0.08), and  $\sin(h) = \sin(\delta)\sin(\phi) + \cos(\delta)\cos(\phi)\cos(AH)$  where  $\delta$  is the solar declination,  $\phi$  is latitude, and  $AH$  is hour angle. To take nebulosity into account, a mean atmospheric attenuation coefficient  $\bar{k}$  was calculated for each day by dividing the daily-integrated solar irradiance (calculated with a LI-COR 190SA quantum sensors on the shore of South Bay and Suisun Bay) by the calculated clear-sky irradiance for each bay. Incident irradiance ( $R_S = R_S \bar{k}$ ) was calculated at each time-step ( $\Delta t = 1$  hour) and at each node of the spatial mesh-grid ( $\Delta x, \Delta y$ ), and was thus noted  $R_S = R_S(x, y, t)$ .

We then used the  $M = 500$  bootstrap replicates  $\theta^*$  to compute  $M = 500$  values of the daily areal productivity for each bay,

$$P_b^{B*} = \sum_{t=1}^T \sum_{x=1}^X \sum_{y=1}^Y p_{\max}^B \tanh\left(\frac{R_S(x, y, t)}{E_k}\right) \Delta t \Delta x \Delta y$$

$$m = 1, \dots, M \quad (3)$$

We were able to calculate the mean and the variance of the daily carbon assimilation rate for each embayment. In order to compare the productivity estimates, the mean potential productivity per unit of area  $\bar{P}_P^B$  was calculated as  $P_b^{B*}$  divided by the intertidal area of each bay.

#### Results and Discussion

##### SPATIAL VARIABILITY OF THE P-I CURVE PARAMETERS

The local estimates of  $\theta = \{\hat{p}_{\max}^B, \hat{E}_k\}$  and  $\hat{SE}(\theta)$  are given in Table 1. Figure 4 compares the experimental results with fitted curves for the photosynthetic measurements performed in each sub-

TABLE 1. Estimates of the parameters  $E_k$  ( $W m^{-2}$ ) and  $P_{max}$  ( $mg C (mg chl a)^{-1} h^{-1}$ ) and their bootstrap standard errors in parentheses. The last column gives the correlation coefficient between the estimators of  $E_k$  and  $P_{max}$ .

	$E_k$	$P_{max}$	Correlation
South Bay	125.25 (6.27)	4.70 (0.10)	0.81
San Pablo Bay	80.57 (8.28)	3.22 (0.12)	0.70
Suisun Bay	66.33 (6.29)	2.30 (0.07)	0.53

basin. Only small differences were observed between the local duplicates, so we estimated only one set of parameters per sub-basin from the pooled data set. Table 1 shows that both  $p_{max}^B$  and  $E_k$  estimates followed the same pattern: South Bay > San Pablo Bay > Suisun Bay. The photosynthetic efficiency  $\alpha$  did not vary among embayments.

A statistical analysis was performed to determine whether the photosynthetic characteristics of the microphytobenthic communities differed significantly among sub-basins (a detailed description of the procedure is presented in Blanchard et al. 1997). We tested the null hypothesis  $H_0$ , the P-E

function parameters are identical, against the alternative hypothesis  $H_1$ , at least one set of the P-E function parameters differs from the other(s). The test relies upon the bootstrap estimate of the null distribution of the following f statistic:

$$f = \frac{(RSS_0 - RSS_1)/(v_0 - v_1)}{RSS_1/v_1} \quad (4)$$

where

$$RSS_0 = \sum_{n=1}^N [P_n - \varphi(E_n, \hat{\theta}_0)]^2, \quad N = \sum_{j=1}^J N_j$$

$$RSS_1 = \sum_{j=1}^J \sum_{i=1}^{N_j} [P_{i,j} - \varphi(E_{i,j}, \hat{\theta}_j)]^2$$

$RSS_0$  refers to the global pooling of resampled residuals from a unique mean-field P-E model ( $H_0$ ), while  $RSS_1$  involves resampling of residuals from  $J = 3$  local P-E models ( $H_1$ );  $v_0 = N - 2$  and  $v_1 = (N - 2)J$  are the corresponding degrees of freedom.

The bootstrap null distributions of f are super-

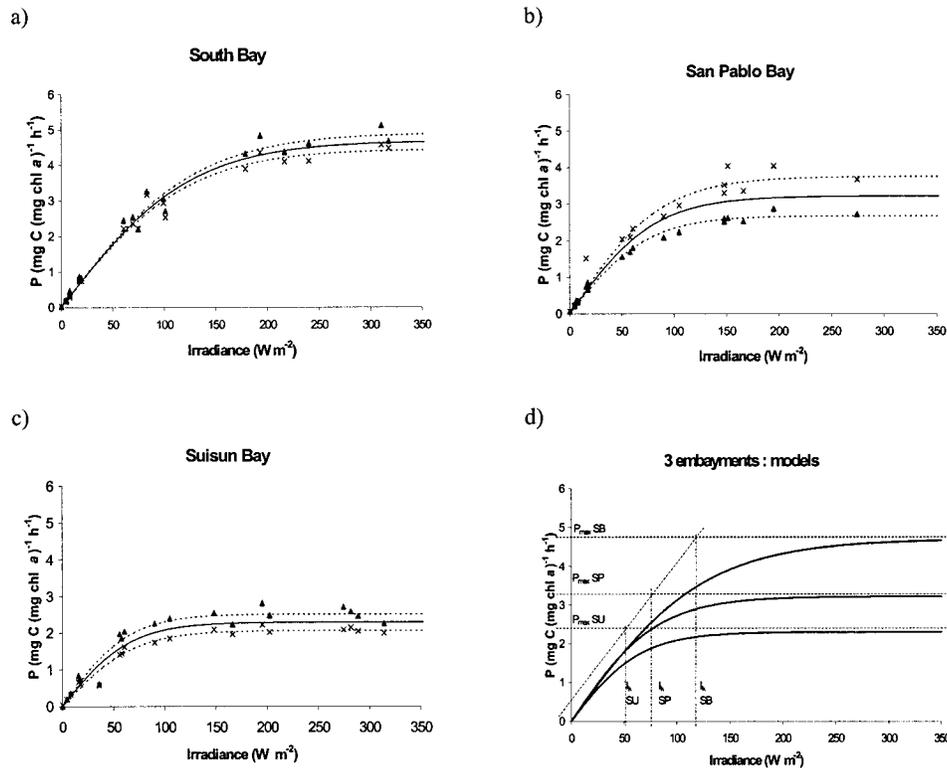


Fig. 4. Fitted P-E curves from experimental data for South Bay, San Pablo Bay, and Suisun Bay. The P-E curve is characterized by three parameters:  $E_k$  (saturation intensity),  $P_{max}^B$  (photosynthetic capacity), and their ratio  $\alpha = E_k/P_{max}^B$  (photosynthetic efficiency). Replicate samples were collected within  $\sim 200$  m at each station (SB, SP, and SU, respectively; see Fig. 1), but only one P-E curve was fitted to the pooled data set from each station. The dotted lines represent the fitted model for the separate data sets represented by two distinct symbols. Summarized pattern of ecophysiological model for the photosynthesis-irradiance relationship in the three different bays.  $E_k$  and  $P_{max}^B$  were higher in South Bay than in San Pablo Bay and Suisun Bay but the photosynthetic efficiency was equal in all 3 embayments.

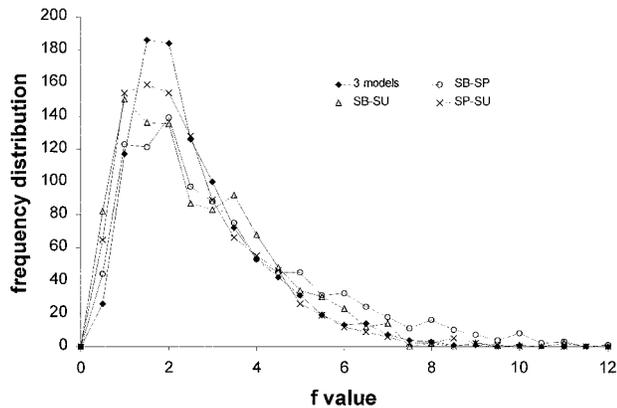


Fig. 5. Null distribution estimates of the  $f$  statistic, using the bootstrap method and testing the null hypothesis  $H_0$  that there is no difference between different models. This  $f$ -statistic was used to compare the three photosynthesis-irradiance relationships in the three different embayments. Critical values  $f_{obs}$  were determined by the optimal fitted curves on the initial data set (see details in text). Four cases are studied: comparison of the three different situations, and comparison of two-by-two situations as indicated in the inserted legend. In all cases, the probability  $p = \text{prob}(f \geq f_{obs} | H_0)$  was near-zero, providing strong evidence against  $H_0$ . Ecophysiological characteristics of each community were significantly different among the three sub-basins of San Francisco Bay.

imposed on Fig. 5 (both for global and pair wise comparisons); the conclusions were drawn from the estimated probabilities of exceeding the statistic values  $f_{obs}$  computed on the experimental measurements. We compared the three different models. The probability,  $\text{prob}(f \geq f_{obs} | H_0)$ , of exceeding  $f_{obs} = 133$  was close to zero. This is strong evidence to refute the null hypothesis that there is no difference of photosynthetic characteristics between microphytobenthic communities of the different sub-basins of San Francisco Bay. If the models are compared pair wise, the results remain the same and the null hypothesis is still rejected.

This analysis shows statistically significant regional differences in the photosynthetic competence of the microalgal communities within the San Francisco Bay intertidal ecosystem. The underlying mechanisms are not evident from our study alone, although this heterogeneity could be the result of spatial differences in water chemistry that parallel the estuarine salinity gradient (Admiraal 1977; Rasmussen et al. 1983) or spatial differences in microalgal community composition (Table 2). From the samples collected in September and October 1998, the dominant species were *Navicula crucicola* and *Nitzschia fonticola* in South Bay, *Gyrosigma balticum* and *Nitzschia cylindrotheca* in San Pablo Bay, and *Navicula cincta* in Suisun Bay.

#### SPATIAL VARIABILITY OF MICROPHYTOBENTHIC POTENTIAL PRODUCTIVITY $\bar{P}_r^B$

The final step of our analysis was to estimate the intertidal microphytobenthic potential productivity and its variability for each embayment. We investigated the effect of the differences in photosynthetic characteristics of each community on the primary productivity of the whole ecosystem. We assumed that ecophysiological characteristics do not vary within the same embayment and we calculated the relative productivity of each sub-basin  $\bar{P}_r^B$  and its variability  $\text{Var}(\bar{P}_r^B)$  from the 500 previous bootstrap replicates of P-E parameter estimates. The frequency distributions of potential productivity in each embayment are compared in Fig. 6. The confidence interval (with an expected error of 0.05) was calculated from the standard error estimates (Table 3). In South Bay, the daily carbon assimilation rate  $P^B$  was  $16.4 \pm 0.9$  mg C (mg chl  $a$ )<sup>-1</sup> d<sup>-1</sup>, higher than in San Pablo Bay ( $7.2 \pm 0.8$  mg C (mg chl  $a$ )<sup>-1</sup> d<sup>-1</sup>) which was higher than Suisun Bay ( $4.0 \pm 0.8$  mg C (mg chl  $a$ )<sup>-1</sup> d<sup>-1</sup>). The frequency distributions of the bootstrap replicates of  $\bar{P}_r^{B*}$  were completely distinct from one bay to another, and we conclude that the mean daily potential productivity ( $\bar{P}_r^B$ ) was significantly different among embayments.

An important outcome of this analysis was that the differences in daily productivity  $\bar{P}_r^B$  were greater than the differences in the P-E parameters among embayments, suggesting that sub-basin differences in potential productivity are not completely explained by physiological differences in the microphytobenthos. In South Bay,  $\hat{p}_{max}^B$  was  $\sim 1.5$  times higher than in San Pablo Bay and  $\sim 2$  times higher than in Suisun Bay. However, the daily carbon assimilation rate  $\bar{P}_r^B$  in South Bay was  $\sim 2.5$  times higher than in San Pablo Bay and  $\sim 4$  times higher than in Suisun Bay. This sub-basin variability of potential productivity may come from differences in the light intensity and/or the duration of light exposure of the intertidal zones of the different embayments. We calculated the proportion of time when the PAR exceeded  $E_k$  during the daytime emersion period (Table 3). In South Bay, this proportion was 94%, lower than in San Pablo Bay (95.5%) and Suisun Bay (96%). These high proportions suggest that light intensity does not play an important role in regulating productivity. The differences between bays were even weaker since the photosynthetic efficiency ( $\alpha$ ) was constant. By construction of the P-E curves, at any given irradiance superior to zero, photosynthetic rate is always equal or higher in South Bay than in San Pablo Bay and Suisun Bay.

As a second measure of the light resource, we

TABLE 2. Species composition in density (number of cells ml<sup>-1</sup>) and biovolume (μm<sup>3</sup> ml<sup>-1</sup>) for the three embayments (South Bay, San Pablo Bay, and Suisun Bay). Main species are in bold.

Sample Site	South Bay		San Pablo Bay		Suisun Bay	
	Density	Volume	Density	Volume	Density	Volume
Bacillariophyceae						
<i>Navicula capitata</i> var. <i>hungarica</i>	18	945			3,212	476,039
<b><i>Navicula cincta</i></b>	193	32,825			<b>137,272</b>	<b>24,157,572</b>
<i>Navicula halophila</i>	210	41,698				
<i>Navicula marginalithii</i>	70	72,979				
<i>Navicula paramutica</i>	18	1,360				
<i>Navicula phyllepta</i>	228	48,412				
<i>Navicula arenaria</i>	53	68,608				
<i>Nitzschia fonticola</i>	2,538	460,404				
<i>Nitzschia inconspicua</i>	18	469				
<i>Nitzschia palea</i>	53	11,615				
<i>Cylindrotheca gracilis</i>	53	30,989				
<i>Surirella</i> sp.	53	36,195				
<b><i>Navicula crucicula</i> f. <i>rostrata</i></b>	<b>5,285</b>	<b>1,066,724</b>	2,862	868,900		
<i>Navicula cryptocephala</i>	263	62,160	304	92,634		
<b><i>Navicula gregaria</i></b>	<b>1,418</b>	<b>1,816,498</b>	114	4,943		
<i>Navicula veneta</i>	18	5,801	2,862	599,833		
<i>Nitzschia distans</i>	105	26,638	43	13,437		
<i>Navicula decussis</i>			130	246,214		
<i>Skeletonema costatum</i>			119	7,951		
<b><i>Gyrosigma balticum</i></b>			<b>596</b>	<b>4,062,587</b>		
<i>Gyrosigma fasciola</i>			40	262,782		
<i>Achnanthes</i> sp.			60	1,335		
<b><i>Nitzschia (Cylindrotheca) closterium</i></b>			<b>8,158</b>	<b>5,240,924</b>		
<i>Nitzschia bacillum</i>			87	21,363	<b>19,258</b>	<b>1,783,291</b>
<i>Nitzschia calida</i>					493	1,543,832
<i>Nitzschia capitellata</i>					459	902,373
<b><i>Nitzschia littoralis</i></b>					<b>303</b>	<b>2,006,945</b>
<i>Nitzschia panduriformis</i> var. <i>delicatula</i>					225	506,295
<i>Nitzschia sigma</i>					190	42,992
<i>Nitzschia hungarica</i>					95	46,477
<i>Nitzschia angustatula</i>					95	12,547
<i>Navicula lanceolata</i>					268	247,293
<i>Cyclotella meneghiniana</i>					95	28,488
Total	10,588	3,784,321	15,374	11,422,902	161,966	31,754,143

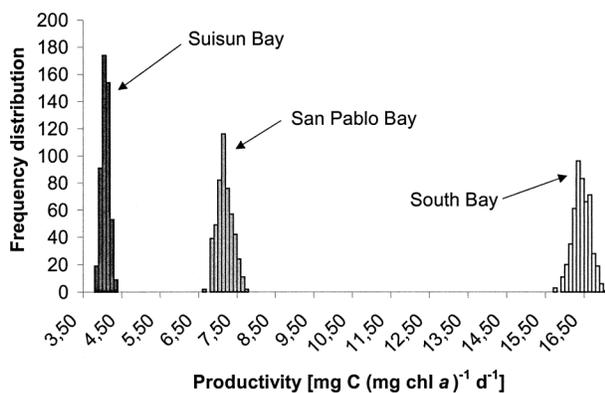


Fig. 6. Productivity estimates for the three different embayments, calculated by using the  $M = 500$  bootstrap replicates  $\theta = \{\hat{P}_{max}^b, \hat{E}_k^b\}$  from the fitted P-E curves (Fig. 2). Productivity in South Bay was significantly higher than in San Pablo Bay and Suisun Bay, and the differences were larger than those explained by differences in the P-E curves suggesting a strong influence of the morphometry of each embayment and the tidal forcing.

calculated the mean duration of the daytime emersion period, which is an indicator of the duration of production for each embayment. In South Bay, this period was 5.4 h (Table 3) and was higher than in San Pablo Bay (4.1 h) and Suisun Bay (3.8 h). This indicates that the mudflat bathymetry and/or the tidal synchronizing cause sub-basin differences

TABLE 3. Productivity estimates for each embayment, using P-E curves. The standard error (in parentheses) was determined from  $M = 500$  bootstrap replicates of parameter sets. The second column presents the total surface of the intertidal area in each bay and the two last columns give the calculation of the proportion of daytime emersion period when light intensities were superior to  $E_k$  (Table 1) and the averaged duration (h) of the daytime emersion period during the fall season.

	$P^b$ mg C (mg chl a) <sup>-1</sup> d <sup>-1</sup>	Surface Area (km <sup>2</sup> )	Proportion E > E <sub>k</sub>	Mean Emersion Time (h)
South Bay	16.4 (0.4)	86	94%	5.4
San Pablo Bay	7.2 (0.4)	45	95%	4.1
Suisun Bay	4.0 (0.2)	6	96%	3.8

in the duration of light exposure to the intertidal surface. These differences in the timing of light exposure appear to play a more important role in controlling the microphytobenthic potential productivity than the light intensity.

### Conclusions

The modeling approach described here, which combines deterministic processes (water elevation, light-dark cycle) and stochastic processes (carbon assimilation of the microalgal community), estimates the potential productivity of intertidal microphytobenthos at the level of the ecosystem. We illustrate a procedure for assessing spatial differences of potential productivity from the experimental determination of few P-E curves parameters; bootstrap methods are used to estimate the variances of measured photosynthesis and calculated rates of areal primary productivity by the benthic microalgae. Results of this preliminary study in San Francisco Bay show that there can be substantial spatial variability in the rate of microphytobenthos primary production within large tidal estuaries. This variability has two important components: spatial variability in the community composition/physiological state of the microphytobenthos, and spatial variations in the propagation of the tidal wave and its influence on the timing and duration of light exposure to the intertidal habitats. Within the San Francisco Bay system, the second source of variability is just as important as the first and it must be considered in estimates of the contribution of microphytobenthos photosynthesis to carbon budgets of the entire estuary. We plan to apply this procedure on a seasonal basis in San Francisco Bay to test the hypotheses that microphytobenthos primary productivity is a significant source of organic matter and that there are significant spatial differences in the annual rate of microphytobenthos primary production within this estuary (Jassby et al. 1993).

### ACKNOWLEDGMENTS

We are pleased to express our gratitude to our friends and colleagues Andy Arnsberg, Tara Schraga, and Brian Cole who helped us so much in the realization of this work; Richard Smith who provided the bathymetric data set for San Francisco Bay; Jeff Gartner who shared computer programs for calculating tidal elevations; and Richard Dufford who performed the taxonomic identification and counting of the microphytobenthos. We thank Rick Oltmann for sharing light measurements in Suisun Bay and Brian Cole for light measurements in South Bay. We are also very grateful to Louise Vicencio and Steve Chappell who gave us access to the study sites.

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*Received for consideration, August 11, 2000*

*Accepted for publication, December 10, 2001*